

Use of a wave tank to study the effects of water motion and algal movement on the displacement of the sea star *Asterias vulgaris* towards its prey

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ABSTRACT: We carried out experiments in a wave tank using a factorial design (in the presence and absence of waves and kelp blades) to evaluate the impact of water motion, and of wave-induced movement of kelp blades, on (1) movement of the predatory sea star *Asterias vulgaris* towards its prey, the blue mussel *Mytilus edulis*, and (2) on its success in capturing its prey. The wave tank mimicked the back-and-forth flow caused by waves. The displacement of the sea stars was 2 times greater in the absence than in the presence of waves. Movements of *A. vulgaris* were more directed towards the prey under back-and-forth water movement than under still conditions. The presence of kelp blades without waves also reduced the movement of sea stars towards prey as the sea stars largely stayed in the portion of the tank without kelp. Sea stars only became detached in treatments with waves, and a greater proportion detached when both waves and kelp were present. The success rate of sea stars in capturing mussels was null in the treatment with both waves and kelp. These observations support the hypothesis that the kelp canopy in shallow water, and movement of the kelp blades by waves, provide mussels with a spatial refuge from sea star predation. We show for the first time that a sea star can use distance chemodetection to localize prey under conditions of back-and-forth flow.

KEY WORDS: Water motion · Kelp movement · Mussels · *Mytilus edulis* · Feeding ecology · Oscillatory flow · *Alaria esculenta* · Spatial refuge · Turbulence

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INTRODUCTION

Water flow and wave action can affect the behavioral repertoire of animals (e.g. movement and feeding rates; Rochette et al. 1994, Kawamata 1998, Jenkins & Hartnoll 2001) and in turn influence species interactions (e.g. predation, herbivory, competition, facilitation; Lubchenco & Menge 1978, Cowen et al. 1982, Witman 1987, Menge et al. 1994). Sessile marine organisms in coastal areas are subjected to multiple hydrodynamic forces (e.g. drag, lift and acceleration forces) exerted by currents and waves (Koehl 1982, Denny 1988, 1995, Denny & Wethey 2001). The magnitude of such forces varies with position on the shore, being much stronger and less predictable in turbulent flows in the intertidal and upper subtidal zones than in deeper water (Denny 1988, Witman & Dayton 2001).

The shoreward wave surge in shallow water is followed by a seaward backwash once the wave has broken (Koehl 1982) so that bottom organisms are subjected to an oscillating, bidirectional flow. In such environments, the risk of being dislodged varies with the shape, size, and texture of the organism as well as with the intensity of the water motion (Koehl 1982, Denny 1995). Many studies comparing data from wave-exposed and wave-sheltered environments ascribe differences in species morphology, distribution, and interactions to the direct effect of water motion (e.g. Southward & Orton 1954, Boulding & Van Alstyne 1993, Trussel et al. 1993, Jenkins & Hartnoll 2001). However, organisms may also be influenced indirectly by water motion, and specifically by wave-induced movement of other organisms. For example, several studies indicate the movement of algal fronds

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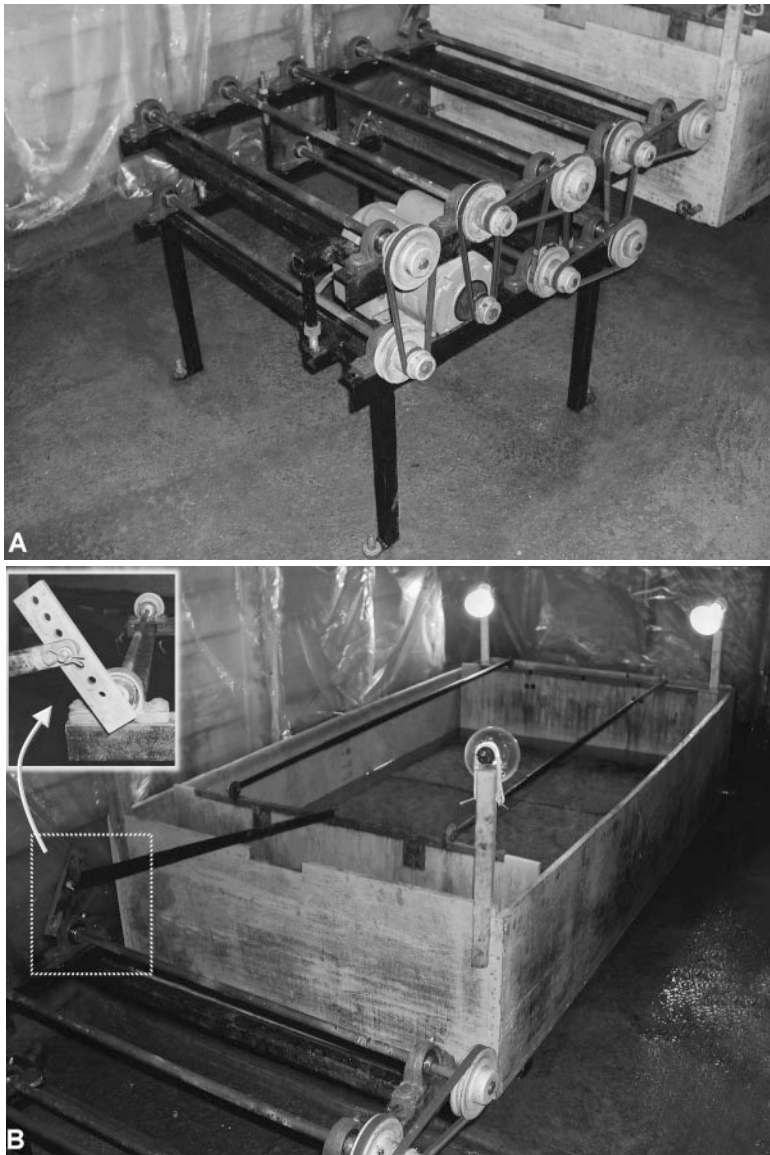


Fig. 1. Wave tank system. (A) The rotational force generated by a 2 HP electric motor is transmitted through a series of pillow blocks, axles, pulleys, and belts. (B) A perforated bar welded to the last axle (enlarged in the upper-left corner, reverse view) is connected to the nearest of 2 plywood panels hinged to the bottom of the wave tank. Two metal bars connecting the top of the first panel with the top of the second causes the 2 panels to move back and forth in parallel, producing oscillating waves

repulses advances by foraging urchins (Himmelman & Steele 1971, Velimirov & Griffiths 1979, Himmelman 1984, Dayton 1985, Vasquez & McPeak 1998, Konar 2000, Gagnon et al. 2003). Despite indications that water motion might shape marine communities by promoting a cascade of species interactions, few workers have attempted to identify and quantify mechanisms that influence the feeding ecology of organisms subjected to variations in water movement.

In the Mingan Islands, northern Gulf of St. Lawrence, the sea stars *Asterias vulgaris* and *Leptasterias polaris* are major predators in the rocky subtidal zone. Their upper limit generally coincides with the lower limit of dense kelp beds (*Alaria esculenta* and *Laminaria* spp.), and few sea stars occur within the kelp beds (Dutil 1988, Himmelman & Dutil 1991, Gaymer et al. 2001a,b). The distribution of their preferred prey, the blue mussel *Mytilus edulis*, is largely restricted to within the kelp canopy (where mussels often densely cover the bottom), and few mussels are found below the kelp zone (Dutil 1988, Himmelman & Dutil 1991, Gaymer et al. 2001a,b). Sea stars forage intensively on mussels in the Mingan Islands (Gaymer et al. 2001a, Gaymer & Himmelman 2002). They rapidly devour patches of mussels in areas not covered by macrophytes and then move on. Although observations suggest *M. edulis* recruiting in the kelp zone may benefit from a spatial refuge from sea star predation, this hypothesis needs to be tested by studies examining whether water motion and algal movement deter sea stars from exploiting mussels under the kelp canopy.

In this study, we use a wave tank to evaluate the impact of waves and of wave-induced movement of algal fronds on (1) movement of the sea star *A. vulgaris* towards its prey and (2) success of the sea star in capturing prey.

MATERIALS AND METHODS

Our study was carried out in a wet laboratory at Havre-Saint-Pierre in the Mingan Islands (50° 13' 6" N, 63° 41' 12" W) in the northern Gulf of St. Lawrence, eastern Canada. The experiments were performed with *Asterias vulgaris* (10 to 15 cm in diameter) collected on 14 July 2001 at 9 to 11 m depth from a bedrock platform on the eastern side of Île aux Goélands. They were maintained for 3 wk (until 2 August 2001) in a large circular tank (1.45 m diameter, 25 cm depth) supplied with mussels as food once a week and a constant inflow of seawater (between 4 and 6°C) pumped from 10 m depth.

Wave tank system. To reproduce the back-and-forth water flow in shallow areas, we developed a device that generated oscillating waves. The apparatus con-

sisted of a 2 HP electric motor (1740 rpm) coupled to a series of pulleys (attached with pillow blocks to a 2-storied iron rack) that reduced the rotation speed of the motor (Fig. 1A). This rotational force was converted into a bi-directional force that moved 2 plywood panels (1.2×0.5 m) in the wave tank ($2.4 \times 1.22 \times 0.48$ m) to produce waves. The panels were hinged to the bottom of the tank at a distance of 0.22 m from the ends of the tank (Fig. 1B). The panels moved in parallel because of 2 metal bars connecting the tops of the panels (attached with swivel cased-bearings). Another metal rod connected the top of the panel closest to the pulley system to a perforated bar welded to the last axle (Fig. 1B). A 1 cm wide gap between the panels and the sides and bottom of the wave tank allowed the water to circulate from one side of the panels to the other. The amplitude of the waves created in the tank could be varied with (1) the depth of water in the tank, (2) the speed of rotation of the axles, as determined by pulleys used, and (3) the position on the perforated bar to which the bar connecting the one panel was attached.

Experimental design. The experiments were carried out between 3 and 23 August 2001. We used a factorial experimental design with 4 treatments: (1) absence of waves and kelp, (2) presence of kelp only, (3) presence of waves only, and (4) presence of waves and kelp. Each treatment was repeated 6 times (thus 24 trials), and each trial was performed in the same wave tank (the order of the trials was determined at random). Five sea stars were used in each trial.

The bottom of the wave tank between the oscillating panels was completely covered by a 2×3 grid arrangement of concrete tiles ($60 \times 60 \times 5$ cm). The upper surface of the tiles was sculpted with holes, cracks, and waves to simulate natural substratum heterogeneity. The experimental area was illuminated by a light bulb (150 W, 1545 lumens, 120° beam; Floodlight, model BR40, Sylvania) at each of the 4 corners of the tank and 90 cm above the bottom. All trials involved mussels 3 to 5 cm in length (attached to 15×15 cm ceramic plates, 22 to 25 mussels per plate) placed in a line across the tank (Fig. 2A). In the treatments with algae, a line of kelp *Alaria esculenta* (40 to 50 cm in length) was placed 5 cm from the line of mussels (Fig. 2B). The stipes of *A. esculenta* were wedged into a split (at 2 to 3 cm intervals) made along a rubber hose

(1.22 m in length, 2.6 cm in diameter). We wound electrical tape around the hose to hold the stipes in the split. The stipes were oriented at an angle of ca. 45° to the bottom of the tank (towards the mussels) so that the outer portions of the blades touched the bottom of the tank. The hose was weighed down by 3×5 kg lead weights. The kelp blades were placed at an angle because of the shallow depth of the tank. In this position the blade tips touched the bottom, mimicking what happens with kelp plants at the lower edge of the kelp fringe. We also changed the mussel lines for each trial (each time randomly choosing 8 plates from 24 available plates), and alternated between 2 hoses with kelp (one with 186 stipes, the other with 194

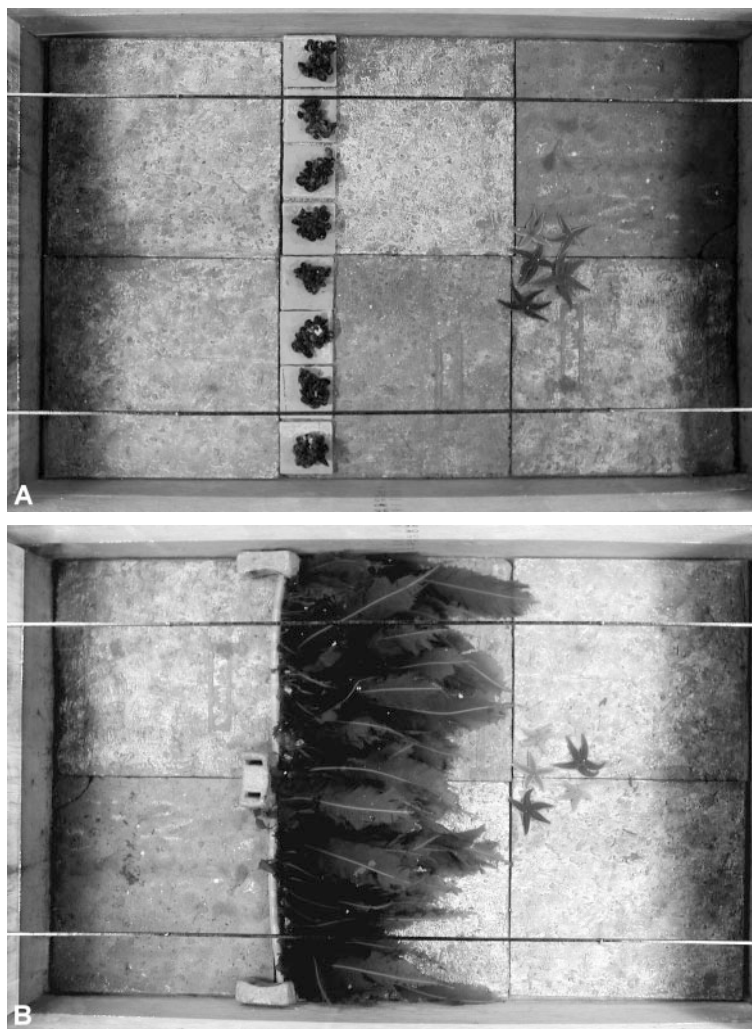


Fig. 2. *Asterias vulgaris*. Experimental setup used in the sea star experiments. The initial position of the 5 sea stars (50 to 55 cm from the line of mussels *Mytilus edulis*) is illustrated for (A) no kelp *Alaria esculenta*, and (B) with kelp treatments. The line of kelp was located 5 cm beyond the mussels and the stipes were oriented so that the blades covered the mussels and the blade tips touched the bottom of the tank

stipes). The pulley system was set up so the system generated 23 wave cycles per minute. This caused the kelp blades to sweep over a 20 cm wide zone. This was ecologically realistic, as we noted wave frequency was ca. 24 waves min^{-1} during moderate (28 km h^{-1}) winds. At this wind strength, kelp at 3 to 5 m depth sweep a zone of 15 to 30 cm in width. To eliminate possible biases due to asymmetries in the conditions around the tank (e.g. light), the side of the tank where the line of mussels was placed was alternated with each new trial. Each trial was carried out with new water (2 to 4°C) and 5 new sea stars.

For each trial, the 5 sea stars were first placed in a group 50 to 55 cm (mean = 52 cm) from the mussels (Fig. 2). We recorded the distance of each sea star (nearest arm tip) to the line of mussels with a ruler (Time 0), and subsequently at 30, 60 and 90 min. At the end of each trial (90 min) we recorded the proportion of 5 sea stars that had their arms wrapped around a mussel, which we considered as feeding activity. In the wave treatments, the motor was only turned on after a delay of 2 min so that sea stars could attach to the bottom.

Flow pattern and forces in the tank. To characterize the flow pattern and provide an indication of the forces to which the sea stars were exposed, we recorded (over 1 min) current velocities in the tank in the waves-only treatment using a Doppler current meter (Vector Current Meter, Nortek). The current meter was placed in a horizontal position in the tank, which permitted recording flow at 10 cm above the bottom, in the center of the tank (8 readings s^{-1}). It was not possible to place the current meter vertically to obtain measurements at the level of the sea stars because of the shallow depth of the tank. The velocity data recorded, u , v , and w (in the x -, y -, and z -direction, respectively), were used to calculate the Reynolds number (Re) for flow in each direction. The higher the Reynolds number, the greater the importance of inertial forces as compared to viscous forces, and thus the greater the shear stress acting on organisms in the tank (Denny 1988). To obtain the average velocity (V_{avg}) in each direction (required in the calculation of Re), we used the equation $|V_{\text{avg}}| = 2|V_0|/\pi$, where V_0 is the maximal recorded velocity (-0.31 , 0.16 , and -0.078 m s^{-1} in the x -, y -, and z -direction, respectively). We calculated Re values using the equation:

$$\text{Re} = \rho u L_{\text{characteristic}}/\mu$$

from Denny (1988), where ρ is the density of sea water at 5°C (1027.7 kg m^{-3} , Chemical Rubber Company 1998), u (or v or w) is the average velocity (0.20 , 0.10 , and 0.05 m s^{-1} , respectively), $L_{\text{characteristic}}$ is the average dimension of the sea stars in the x -, y - and z -direction (0.14 , 0.14 , and 0.02 m , respectively), and μ is the dynamic viscosity of sea water at 5°C ($1.610 \times 10^{-3} \text{ N s m}^{-2}$, Chemical Rubber Company 1998).

Statistical analysis. We applied a repeated measures ANOVA (Hand & Taylor 1987, Crowder & Hand 1990) to examine the effect of water motion and kelp movement on the displacement of *Asterias vulgaris* with the factors Waves (with and without), Kelp (with and without *Alaria esculenta*), and Time (after 30, 60 and 90 min). Since variances were similar over time within any treatment and the correlation in the data over time was similar for all treatments, we used a pooled covariance structure in the ANOVA (Proc Mixed, type = CS, SAS Institute 1999). Prior to the analyses, the data were square-root transformed to obtain normal distributions for each observation time. Normality was verified using Shapiro-Wilk's statistic (SAS Institute 1999) and the homogeneity of within-treatment covariance matrices was tested using Box's test (Proc Discrim, SAS Institute 1999, Rencher 1995).

We performed a 2-way ANOVA (Zar 1999) to study the effect of water motion and kelp movement on the distance of the sea stars to the mussels (factors = Waves and Kelp). The analysis was applied to the raw data that were normally distributed. In this analysis, normality was verified using Shapiro-Wilk's statistic (SAS Institute 1999) and homoscedasticity by examining the graphical distribution of the residuals and by using Levene tests (Snedecor & Cochran 1989).

We used a 2-way ANOVA to analyze the effect of water motion and kelp movement on the success of *Asterias vulgaris* in capturing prey (factors = Waves and Kelp). We treated this analysis as a particular case of the generalized linear models (Proc Genmod, SAS Institute 1999, McCullagh & Nelder 1989) which assumed a binomial distribution of the response variable (prey capture or not), and thus did not test for normality and homoscedasticity in the data. In all these analyses, differences between levels within a factor

Table 1. Summary of the repeated measures ANOVA (mixed linear model applied to square-root transformed data) showing the effect of Waves (with or without), Kelp (presence or absence of *Alaria esculenta*), and Time (observations after 30, 60 and 90 min) on the mean displacement of the sea star *Asterias vulgaris*

Source of variation (fixed effects)	df	F	p
Waves	1,20	47.19	<0.001
Kelp	1,20	5.94	0.024
Time	2,40	6.83	0.0028
Waves \times Kelp	1,20	2.55	0.13
Waves \times Time	2,40	4.11	0.024
Kelp \times Time	2,40	3.89	0.029
Waves \times Kelp \times Time	2,40	2.38	0.11

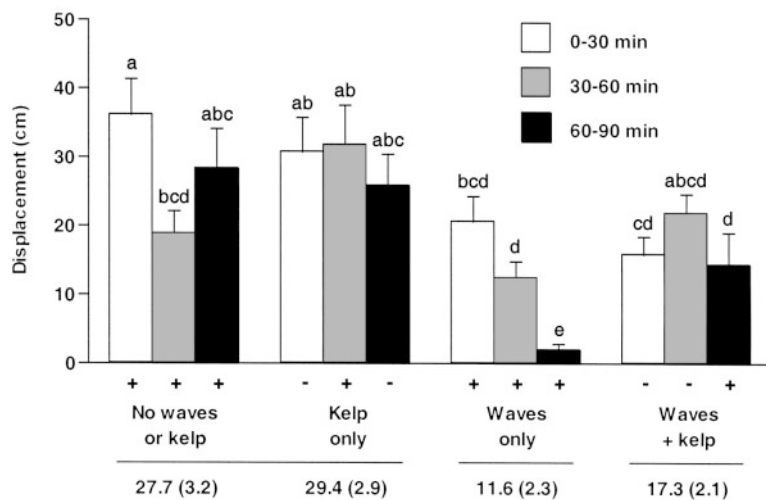


Fig. 3. *Asterias vulgaris*. Mean perpendicular displacement (+SE) of sea stars during 3 consecutive 30 min intervals in trials examining the effect of the absence or presence of waves and kelp *Alaria esculenta*. Data have been back-transformed from the square-root transformed data used in the analysis. Values at the bottom are the mean distances (\pm SE) moved for the 3×30 min intervals. The symbols under the columns indicate whether mean displacement was towards (+) or away (-) from the prey. Bars not sharing the same letter, and treatments not bracketed by the same horizontal line (at the bottom) are different (least-square means tests, $p < 0.05$)

were detected using least-square means multiple comparisons tests (LS means, SAS Institute 1999) and the significance threshold of 0.05 was used for all statistical tests.

RESULTS

Measurements of mean distance moved by sea stars over 3 consecutive 30 min intervals indicated that waves severely limited the movement of *Asterias vulgaris* (Table 1, Fig. 3). For example, in the 2 treatments without kelp, overall movement (the mean for the 3 intervals) was more than twice as great when waves were absent (27.7 cm) than when they were present (11.6 cm). Movement in the presence of kelp without waves (29.4 cm) was about the same as in the absence of waves and kelp (LS means, $p = 0.56$). Surprisingly, movement was greater in the presence of kelp and waves (17.3 cm) than with waves alone. Further differences between the last 2 treatments were seen in the changes in displacement over the 3 consecutive 30 min intervals. Displace-

ment was about the same in the 3 intervals in the treatment with waves and kelp. In contrast, displacement progressively decreased in the treatment with waves alone, and the sea stars almost did not move during the final 30 min period. Whereas no sea stars detached in the 2 treatments without waves, 3 (10%) detached in the waves-only treatment and 7 (23.3%) in the waves-plus-kelp treatment. The current meter data on flow in the waves-only treatment indicated that sea stars were submitted to oscillatory flow, with the greatest velocities (peak of 0.31 m s^{-1}) along the longitudinal axis (x -direction, Fig. 4). The sea stars were exposed to a high degree of turbulence that was mostly due to longitudinal flow ($Re = 17\,873$) and, to a lesser extent, to lateral (y -direction) flow ($Re = 8936$) (flow is turbulent when $Re > 2000$, Denny 1988). In contrast, vertical flow (z -direction) was weak (Fig. 4) and laminar ($Re = 638$), and thus probably had little effect on the sea stars.

The mean distance of *Asterias vulgaris* from the line of mussel at the end of the experiments (after 90 min) showed a marked negative effect of kelp on the movement of the sea stars towards the mussels (Table 2, Fig. 5). The mean distance of the sea stars to the mussels in the 2 treatments without kelp was 32.4 to 32.9 cm (Fig. 5). In contrast, the mean distance of the sea stars from the

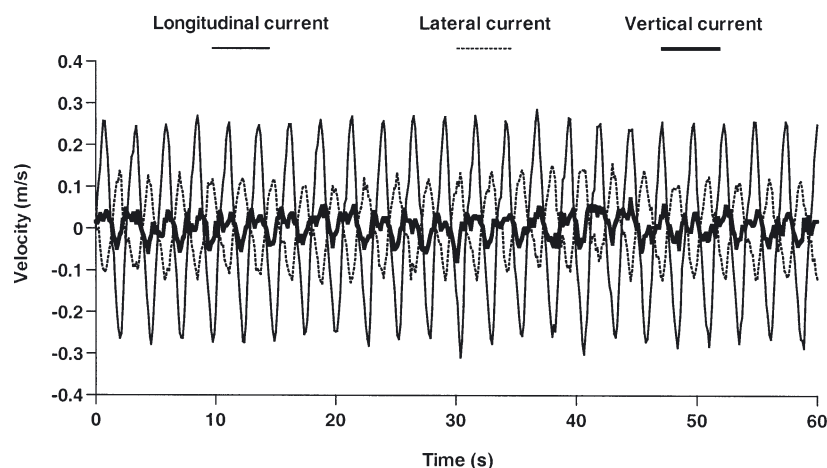


Fig. 4. Cyclic changes in current velocity during wave treatments as documented over a 1 min period with a Doppler current meter (Vector Current Meter, Nortek). Solid, dashed, and bold lines represent longitudinal (x -direction), lateral (y -direction), and vertical (z -direction) current velocities, respectively. Readings were made (8 readings per second) 10 cm above the bottom in the center of the tank (97 cm from each of the oscillating panels)

Table 2. Summary of 2-way ANOVA (applied to raw data) examining the effect of waves (with or without) and kelp (presence or absence of *Alaria esculenta*) on the mean distance of sea stars *Asterias vulgaris* from a line of mussels *Mytilus edulis* at the end of 90 min trials

Source of variation	df	MS	F	p
Waves	1	2.08	0.01	0.93
Kelp	1	2655.11	10.01	<0.01
Waves × Kelp	1	0.16	<0.01	0.98
Error	20	265.12		
Corrected total	23			

mussels at the end of the 2 treatments with kelp (53.3 to 54.1 cm) was almost the same as the distance of the sea stars from the mussels at the beginning of the trials (52.0 cm). The mean displacement of the 5 sea stars in the 2 treatments without kelp was consistently towards the mussels, whereas it was away from the mussels as often as towards them in the treatments with kelp (Fig. 3).

The data on numbers of sea stars with their arms wrapped around a mussel at the end of the experiments (after 90 min) indicate that both waves and kelp decreased prey capture success (Table 3, Fig. 6). The highest proportion of sea stars feeding (33.3%) was in the absence of waves and kelp, and although not statistically different, this proportion was twice that in the presence of kelp only (16.6%, LS means, $p = 0.14$) and

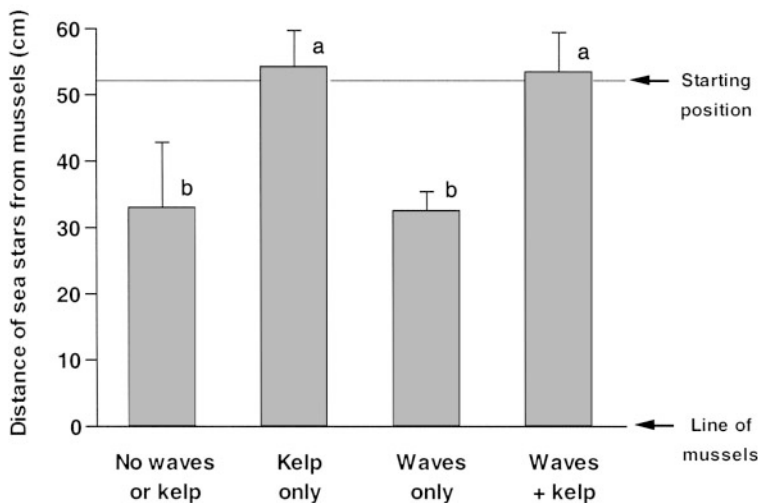


Fig. 5. *Asterias vulgaris*. Mean distance (+SE) of sea stars from their prey at the end of the 90 min trials examining the effect of the absence or presence of waves and kelp *Alaria esculenta*. The horizontal line at 52 cm shows the mean position of the 5 sea stars at the beginning of each trial. Values not sharing the same letter are different (least-square means tests, $p < 0.05$)

Table 3. Summary of 2-way ANOVA (generalized linear model) examining the effect of waves (with or without) and kelp (presence or absence of *Alaria esculenta*) on the success of the sea star *Asterias vulgaris* in capturing a prey (mussel *Mytilus edulis*) at the end of 90 min trials

Source of variation	df	χ^2	p
Waves	1	10.76	0.001
Kelp	1	8.02	0.0046
Waves × Kelp	1	2.49	0.11

with waves only (13.3%, LS means, $p = 0.08$). Waves and kelp together drastically reduced attacks by sea stars (0% feeding, Fig. 6).

DISCUSSION

Although SCUBA diving permits the observation of organisms under natural conditions, it is often difficult to use diving to study the behavior of marine invertebrates because of their slow movement (e.g. sea stars and urchins) and the limited period that can be spent underwater (particularly in cold waters). Further, it is difficult to vary environmental variables in a controlled manner. One alternative is to perform behavioral studies in the laboratory. The design of our wave tank provided several advantages: (1) The system can easily be constructed and at a fraction of the price of hydraulic systems (material costs were ca. \$900 US). (2) The intensity (height) and frequency of the back-and-forth flows can easily be varied. (3) The experimental area is quite large (and could be made larger) so that organisms can be set up in situations resembling natural conditions.

Our studies of the behavior of *Asterias vulgaris* in a wave tank demonstrate the movement of the sea star, and its success in capturing prey (the blue mussel *Mytilus edulis*) is negatively affected by water motion and algal movement. The displacement of the sea stars was more than twice as great in the treatment with no waves and no kelp than in the treatment with waves and no kelp. Surprisingly, in spite of this difference, *A. vulgaris* came to within a similar distance of the mussels in these 2 treatments. This was because the sea stars more often moved towards the prey when there was back-and-forth water movement than in the treatment with no waves or kelp. These observations indicate that chemodetection is more effective in localizing prey when there are waves.

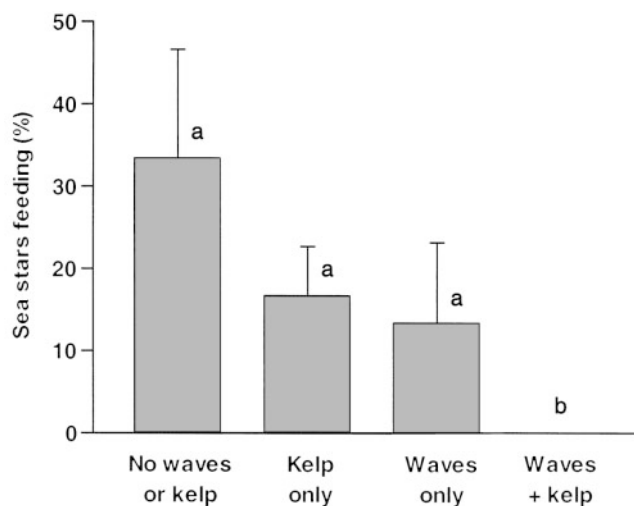


Fig. 6. *Asterias vulgaris* feeding on *Mytilus edulis*. Mean percentage (+SE) of sea stars *A. vulgaris* feeding on the blue mussel *M. edulis*, at the end of 90 min trials examining the effect of the absence or presence of waves and kelp *Alaria esculenta*. Values not sharing the same letter are different (least-square means tests, $p < 0.05$)

Numerous studies indicate sea stars use olfaction to detect prey (see review in Feder & Christensen 1966, Castilla & Crisp 1970, Castilla 1972, Sloan & Campbell 1982, Moore & Lepper 1997). Our results corroborate such studies, indicating the distance chemodetection abilities of *A. vulgaris* (Smith 1940, Zafiriou 1972, Sloan & Campbell 1982). In addition, we show for the first time that *A. vulgaris* can use chemodetection to locate prey even under conditions of back-and-forth water flow. This ability should be highly advantageous for animals such as *A. vulgaris* that often inhabit wave-exposed areas.

At first glance, the nearly identical displacement of *Asterias vulgaris* in the treatments with no waves and no kelp, and with only kelp, suggests kelp did not affect the movement of the sea star. However, in the kelp-only treatment, the sea stars were 39.2% further from the mussels, as they mainly moved in the portion of the tank without kelp blades and were no closer to the mussels at the end than at the start of the experiment. This showed that *A. vulgaris* even avoids moving under non-moving *Alaria esculenta* blades. The proportion of sea stars that detached from the bottom was twice as high in the treatment with waves and kelp than in the treatment with waves alone. This was likely because the sea stars were stimulated to move by the sweeping kelp blades and were thus less well attached. These observations indicate that water motion also decreases the movement of sea stars. The high turbulence in the waves-only trials created shear forces on the sea stars that were greatest when they were moving in a straight line (perpendicu-

larly) towards or away from the mussels. Thus, currents likely limited the movement of sea stars towards the mussels both directly, due to shear forces, and indirectly, by causing movement of kelp blades. The actual shear forces affecting the sea stars in our trials would be slightly less than the forces calculated from our measurements of flow at 10 cm above the bottom. Further, shear forces would be less in the trials with both waves and kelp, because macrophyte canopies reduce flow (Eckman et al. 1989, Ackerman & Okubo 1993). Shear forces would have been virtually null in our 2 treatments without waves. Although studies suggest that wave-induced movement of kelp blades limits movements of (or repulses) mobile consumers (e.g. Himmelman & Steele 1971, Velimirov & Griffiths 1979, Himmelman 1984, Dayton 1985, Vasquez & McPeak 1998, Konar 2000, Gagnon et al. 2003), our study is the first to provide experimental evidence supporting this hypothesis.

The ultimate impact of water motion and kelp movement on *Asterias vulgaris* is to decrease its success in capturing prey. Prey capture is highest in the absence of waves and kelp, drops with the addition of either kelp or waves, and is null when both kelp and waves are present.

Our findings support the hypothesis that the kelp beds in shallow exposed areas in the Mingan Island (the algal fringe) provide the mussel *Mytilus edulis* with a spatial refuge from sea star predation. The inverse distributions of *M. edulis* (restricted to kelp beds) and *Asterias vulgaris* (restricted to the outside of kelp beds), as described by Dutil (1988), Himmelman & Dutil (1991), and Gaymer et al. (2001a,b), appear to occur because waves and algal movement deter sea stars from moving into the kelp zone. Our wave tank could only to some degree mimic the natural environment, and could have over- or under-estimated the impact of waves and algal movement on sea star foraging. Nevertheless, our experiments provided relative measurements of the impact of back-and-forth water motion and kelp movement on the foraging behaviour of *A. vulgaris*. It would be difficult to obtain similar information under field conditions, because it is almost impossible to control water motion, and because of replication problems.

Acknowledgements. This research was supported by NSERC (Natural Sciences and Engineering Research Council of Canada) and FCAR (Fonds pour la Formation de Chercheurs et l'Aide à la Recherche) grants to J.H.H. P.G. was supported by scholarships from NSERC, FCAR and Québec-Océan. We are grateful to C. Gaymer for aid in planning the sea star experiments, to C. Bégin and A. Drouin for their help in the collection of organisms, and to L. E. Johnson for aiding with the use of the Doppler current meter. Thanks also go to G. Gagnon and E. Bernard who helped in the construction of the wave tank, to J.-M. Daigle who provided statistical advice, and to H. Kröger and L. Tremblay for assistance in the calculation of the turbulence in our wave tank.

LITERATURE CITED

- Ackerman JD, Okubo A (1993) Reduced mixing in a marine macrophyte canopy. *Funct Ecol* 7:305–309
- Boulding EG, Van Alstyne KL (1993) Mechanisms of differential survival and growth of two species of *Littorina* on wave-exposed and on protected shores. *J Exp Mar Biol Ecol* 169:139–166
- Castilla JC (1972) Response of *Asterias rubens* to bivalve prey in a Y-maze. *Mar Biol* 12:222–228
- Castilla JC, Crisp DJ (1970) Responses of *Asterias rubens* to olfactory stimuli. *J Mar Biol Assoc UK* 50:829–847
- Chemical Rubber Company (1998) *CRC Handbook of chemistry and physics*. CRC Press, Cleveland, Ohio
- Cowen RK, Agegian CR, Foster MS (1982) The maintenance of community structure in a central California giant kelp forest. *J Exp Mar Biol Ecol* 64:189–201
- Crowder MJ, Hand DJ (1990) *Analysis of repeated measures*. Chapman & Hall, London
- Dayton PK (1985) The structure and regulation of some South American kelp communities. *Ecol Monogr* 55:447–468
- Denny MW (1988) *Biology and the mechanics of the wave-swept environment*. Princeton University Press, Princeton, NJ
- Denny MW (1995) Survival in the surf zone. *Am Sci* 83:166–173
- Denny M, Wethey D (2001) Physical processes that generate patterns in marine communities. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer Associates, Sunderland, MA, p 3–37
- Dutil C (1988) *Partage des ressources alimentaires et comportement de prédation des étoiles de mer de la communauté infralittorale du golfe du Saint-Laurent*. MSc thesis, Université Laval, Québec
- Eckman JE, Duggins DO, Sewell AT (1989) Ecology of understory kelp environments. I. Effects of kelps on flow and particle transport near the bottom. *J Exp Mar Biol Ecol* 129:173–187
- Feder HM, Christensen AM (1966) Aspects of Asteroid biology. In: Boolootian RA (ed) *Physiology of Echinodermata*. Interscience, New York, p 87–127
- Gagnon P, Himmelman JH, Johnson LE (2003) Algal colonization in urchin barrens: defense by association during recruitment of the brown alga *Agarum cribrosum*. *J Exp Mar Biol Ecol* 290:179–196
- Gaymer CF, Himmelman JH (2002) Mussel beds in deeper water provide an unusual situation for competitive interactions between the seastars *Leptasterias polaris* and *Asterias vulgaris*. *J Exp Mar Biol Ecol* 277:13–24
- Gaymer CF, Himmelman JH, Johnson LE (2001a) Distribution and feeding ecology of the seastars *Leptasterias polaris* and *Asterias vulgaris* in the northern Gulf of St. Lawrence, Canada. *J Mar Biol Assoc UK* 81:827–843
- Gaymer CF, Himmelman JH, Johnson LE (2001b) Use of prey resources by the seastars *Leptasterias polaris* and *Asterias vulgaris*: a comparison between field observations and laboratory experiments. *J Exp Mar Biol Ecol* 262:13–30
- Hand DJ, Taylor CC (1987) *Multivariate analysis of variance and repeated measures*. Chapman & Hall, London
- Himmelman JH (1984) Urchin feeding and macroalgal distribution in Newfoundland, eastern Canada. *Nat Can* 111:337–348
- Himmelman JH, Dutil C (1991) Distribution, population structure and feeding of subtidal seastars in the northern Gulf of St. Lawrence. *Mar Ecol Prog Ser* 76:61–72
- Himmelman JH, Steele DH (1971) Foods and predators of the green sea urchin *Strongylocentrotus droebachiensis* in Newfoundland waters. *Mar Biol* 9:315–322
- Jenkins SR, Hartnoll RG (2001) Food supply, grazing activity and growth rate in the limpet *Patella vulgata* L.: a comparison between exposed and sheltered shores. *J Exp Mar Biol Ecol* 258:123–139
- Kawamata S (1998) Effect of wave-induced oscillatory flow on grazing by a subtidal sea urchin *Strongylocentrotus nudus* (A. Agassiz). *J Exp Mar Biol Ecol* 224:31–48
- Koehl MAR (1982) The interaction of moving water and sessile organisms. *Sci Am* 247:124–134
- Konar B (2000) Seasonal inhibitory effects of marine plants on sea urchins: structuring communities the algal way. *Oecologia* 125:208–217
- Lubchenco J, Menge BA (1978) Community development and persistence in a low rocky intertidal zone. *Ecol Monogr* 59:67–94
- McCullagh P, Nelder JA (1989) *Generalized linear models*. Chapman & Hall, New York
- Menge BA, Berlow EL, Blanchette CA, Navarrete SA, Yamada SB (1994) The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol Monogr* 64:249–286
- Moore PA, Lepper DME (1997) Role of chemical signals in the orientation behavior of the sea star *Asterias forbesi*. *Biol Bull* 192:410–417
- Rencher AC (1995) *Methods of multivariate analysis*. John Wiley & Sons, New York
- Rochette R, Hamel JF, Himmelman JH (1994) Foraging strategy of the asteroid *Leptasterias polaris*: role of prey odors, current and feeding status. *Mar Ecol Prog Ser* 106:93–100
- SAS Institute (1999) *SAS/STAT user's guide, Version 8*. SAS Institute, Cary, NC
- Sloan NA, Campbell AC (1982) Perception of food. In: Jangoux M, Lawrence JM (eds) *Echinoderm nutrition*. AA Balkema, Rotterdam, p 3–23
- Smith GFM (1940) Factors limiting distribution and size in the starfish. *J Fish Res Board Can* 5:84–103
- Snedecor GW, Cochran WG (1989) *Statistical methods*. Iowa State University Press, Iowa
- Southward AJ, Orton JH (1954) The effects of wave-action on the distribution and numbers of the commoner plants and animals living on the Plymouth breakwater. *J Mar Biol Assoc UK* 33:1–19
- Trussel GC, Johnson AS, Rudolph SG, Gilfillan ES (1993) Resistance to dislodgment: habitat and size-specific differences in morphology and tenacity in an intertidal snail. *Mar Ecol Prog Ser* 100:135–144
- Vasquez JA, McPeak RH (1998) A new tool for kelp restoration. *Calif Fish Game* 84:149–158
- Velimirov B, Griffiths CL (1979) Wave-induced kelp movement and its importance for community structure. *Bot Mar* 22:169–172
- Witman JD (1987) Subtidal coexistence: storms, grazing, mutualism and the zonation of kelps and mussels. *Ecol Monogr* 57:167–187
- Witman JD, Dayton PK (2001) Rocky subtidal communities. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer Associates, Sunderland, MA, p 339–366
- Zafiriou O (1972) Response of *Asterias vulgaris* to chemical stimuli. *Mar Biol* 17:100–107
- Zar JH (1999) *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ